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Environmental constraint of intraguild predation: Inorganic turbidity modulates omnivory in fairy shrimps

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Abstract

1. Omnivory is widespread in food webs, with an important stabilising effect. The strength of omnivorous trophic interactions may change considerably with changes in the local environment.
2. Shallow temporary waters are often characterised by high levels of inorganic turbidity that may directly limit the food uptake of filter-feeding organisms, but there is little evidence on how it might affect omnivorous species. Anostracans are key species of temporary waters and recent evidence suggests that these organisms are omnivorous consumers of both phyto- and zooplankton.
3. Using *Branchinecta orientalis* as a model species, our aim was to test how turbidity affects the feeding of an omnivorous anostracan. To do this, we used short-term feeding experiments and stable isotope analyses, with animals collected from soda pans in eastern Austria. In the feeding experiments, algae and zooplankton were offered as food either separately or in combination. The prey type treatments were crossed with turbidity levels in a factorial design.
4. There was a pronounced decrease in the ingested algal biomass with increasing turbidity. Conversely, ingestion rates on zooplankton were less affected by turbidity. Stable isotope analyses from field material supported our experimental results by showing a positive relationship of the trophic position of anostracans and the trophic niche of the communities with turbidity.
5. Our results show that turbidity modulates the intraguild trophic relationship between anostracans and their prey by shifting the diet of anostracans from more herbivorous in transparent to more carnivorous in turbid waters. Thus, inorganic turbidity might also have a community-shaping role in plankton communities of temporary waters through altering trophic relationships.

KEYWORDS

anostracans, phytoplankton, temporary ponds, trophic webs, zooplankton

1 | INTRODUCTION

Omnivory, that is feeding on multiple trophic levels (Coll & Guershon, 2002; Pimm & Lawton, 1978), is a very frequent component of all food webs (Holt & Polis, 1997; Kratina, LeCraw, Ingram, & Anholt, 2012; Thompson, Hemberg, Starzomski, & Shurin, 2007). Intraguild predation (IGP) is one type of omnivory, referring to predation on a potential competitor (Arim & Marquet 2004; Polis, Myers, & Holt, 1989). In an IGP system, two predators share a food source (shared prey), thereby acting as competitors. One of them furthermore acts as a predator for the other, being an intraguild predator (IG predator), whereas the preyed competitor is the intraguild prey (IG prey). The feeding of an IG predator may have important influence on community persistence (Stouffer & Bascompte, 2010) and stability (Neutel et al., 2007; Wootton, 2017).

Intraguild predation interactions are not static and their strength varies over time (Wootton, 2017). Besides changes in community composition (e.g. due to dispersal; Amarasekare, 2006) or habitat structure (Anderson & Semlitsch, 2016; Janssen, Sabelis, Magalhaes, Montserrat, & Van der Hammen, 2007), changes in the local environment (Sentis, Hemptinne, & Brodeur, 2014) can alter the strength of the links in IGP systems, as was shown in the case of temperature (Boersma et al., 2016) and productivity (Diehl & Feissel, 2000, 2001). In general, factors that decrease the strength of omnivorous trophic interactions (i.e. the omnivore feeds predominantly on one trophic level) will favour coexistence and increase the stability of food webs (Wootton, 2017). This suggests that the presence of a refuge that decreases the foraging ability of the IG predator on some prey groups will promote species coexistence (Janssen et al., 2007), which has been shown due to the presence and the structuring effect of vegetation (Bell, McCoy, & Mushinsky, 1991), but decreased visibility can also decrease the susceptibility of zooplankton to visual predators (Nurminen & Horppila, 2006; Vinyard & O'Brien, 1976).

Temporary waters are generally shallow and strongly exposed to the mixing effect of wind (Lahr, Diallo, Ndour, Badji, & Diouf, 1999; Naganawa & Zagas, 2002). Besides, they are often visited by large wallowing mammals and waterfowl with obvious consequences for turbidity and mixing (Vanschoenwinkel et al., 2011). As a result, inorganic turbidity is generally high, but may vary considerably among temporary habitats due to differences in depth and macrovegetation cover (Boros, Katalin, Vörös, & Horváth, 2017; Boven, Stoks, Forró, & Brendonck, 2008). As temporary ponds are often dominated by suspension-feeding crustaceans (cladocerans, copepods, anostracans) and rotifers, it raises the question of how these organisms cope with turbid conditions. As suspended inorganic particles (e.g. clay, silt; Eiler et al., 2003) interfere with the filter-feeding process (Kirk & Gilbert, 1990), their high concentration in the water is expected to have a negative effect on zooplankters (Dejen, Vijverberg, Nagelkerke, & Sibbing, 2004; Teffera et al., 2018; Zhou, Qin, & Han, 2018). There is, however, a difference among suspension feeders in their ability of coping with (often extreme) turbid conditions. Non-selective filter feeders such as cladocerans are generally believed to be adversely affected by the high concentration of inorganic suspended particles (but see Hart, 1992), which they ingest together with their food (e.g. bacteria, algae) (Levine, Zehrer, & Burns, 2005; McCabe & O'Brien, 1983). Conversely, rotifers and copepods are more flexible in their feeding mode and can selectively feed on suitable particles, hence they are less affected by inorganic suspended solids than cladocerans (Hart, 1986, 1988; Kirk, 1991a; Kirk & Gilbert, 1990). Compared to cladocerans and copepods, we know much less about the feeding mechanism of anostracans. These flagship species of temporary waters play several key roles in their ecosystems, for example, it is suggested that they interact strongly with zooplankton with consequences for the trophic structure (Waterkeyn, Grillas, Anton-Pardo, Vanschoenwinkel, & Brendonck, 2011), and are also important as food source for waterbirds (Horváth, Vad, Vörös, & Boros, 2013b; Sánchez, Green, & Castellanos, 2006). Recent findings suggest that several anostracan species might act as IG predators in their habitats by preying on zooplankton and at the same time, competing for e.g. algal food (Lukić, Horváth, Vad, & Ptacnik, 2018). Based on their occurrence and habitat preferences, several anostracan species seem to be favoured by turbid conditions (Boudrias & Pires, 2002; Horváth, Vad, Vörös, et al., 2013b; Petkovski, 1991, 1993). For example, the three fairy shrimp species inhabiting Central European soda pans (including our study species *Branchinecta orientalis*) all seem to prefer highly turbid habitats according to field data (Horváth, Vad, Vörös, & Boros, 2013a). Although high turbidity may protect them from visual predators (e.g. amphibians and certain bird species; Boudrias & Pires, 2002; Boven, Vanschoenwinkel, De Roeck, Hulsmans, & Brendonck, 2008; Petkovski, 1993), it could at the same time be a constraint for food uptake by filter-feeding. It therefore seems unclear whether there is a causal relationship beyond predator avoidance behind the occurrence of anostracans in turbid waters, or whether turbidity merely coincides with other factors supporting them.

To date, there is little evidence on how inorganic turbidity affects trophic interactions, and particularly IGP relationships, in temporary ponds. To study whether herbivorous (on algae; shared prey) and carnivorous feeding (on zooplankton; IG prey) of anostracans (IG predator) is affected by increasing turbidity in a similar manner, we first performed controlled laboratory experiments and then compared our results to empirical data from the field. The experimental turbidity gradient in our feeding experiments covered the typical range of turbidity found in our study systems, soda pans. We crossed the turbidity gradient with a treatment of prey type (algae, zooplankton, algae, and zooplankton combined) to study the effect of increasing turbidity on ingestion rates for different food types. We then performed a field test to find empirical support for whether the trophic position of anostracans and the trophic niche of communities (which are expected to shift with changes in the dominant prey type) change along a natural

gradient of turbidity in nine soda pans based on carbon and nitrogen stable isotope analysis.

2 | METHODS

2.1 | Study system—soda pans of the Central European Lowlands

The soda pans of the Central European lowlands (Austria, Hungary, and Serbia) are inland saline waters of non-marine origin. Their ionic composition is dominated by Na^+, CO_3^{2-} and HCO_3^- that is considerably different from sea water (Boros, Ecsedi, & Oláh, 2013). Due to their high surface-to-volume ratio their sediment can easily be stirred up by the mixing effect of winds, consequently the amount of total suspended solids (TSS) can be extremely high, varying from 10 to over 30,000 mg/L (Boros et al., 2013). Particularly at the upper end of this gradient, TSS comprises almost exclusively abiotic and inorganic particles (e.g. clay, silt, sand) (Boros et al., 2017; Somogyi, Pálffy, Balogh, Botta-Dukót, & Vörös, 2017). The systems are naturally hypertrophic with total phosphorus concentrations (TP) ranging between 67 and 58,772 μg/L (measured between 2009 and 2010; Boros et al., 2013). During their wet phase, soda pans and other temporary saline pools on the steppes of Central and Eastern Europe represent a considerable proportion of shallow water habitats. For this reason, soda pans and sodic meadows are important resting sites for numerous waterbirds during their seasonal migration on the north-south route in the Western Palaearctic (Boros et al., 2013; Horváth, Vad, Vörös, et al., 2013b). In general, these systems are fishless, while vegetation is only occasionally present around the shore. The algal and zooplankton density generally increases with TSS in the pans, reaching extremely high abundances (Horváth et al., 2014). Pico-sized unicellular algae are the dominant group of phytoplankton in these systems (Somogyi et al., 2009, 2017). The dominant species of zooplankton are the calanoid copepod *Arctodiaptomus spinosus* and the cladoceran *Moina brachiata*, especially in turbid and saline pans (Horváth et al., 2014).

2.2 | Study species—the fairy shrimp *Branchinecta orientalis*

Branchinecta orientalis inhabits mineral-rich temporary waters and is distributed between 27° and 55°N in Europe and Asia (Mura & Takami, 2000; Padhye, Kulkarni, & Dumont, 2017). Active populations of the species generally occur from March to June but exceptions have also been recorded in late autumn or winter (Atashbar, Agh, Van Stappen, & Beladjal, 2014; Eder, Hödl, & Gottwald, 1997; Petkovski, 1991; Šćiban, Marković, Lukić, & Miličić, 2014). In Central European soda pans, they occur within a wide turbidity range and represent the most frequent and numerous anostracan species (Horváth, Vad, Voeroes, et al., 2013a). *B. orientalis* is an omnivore, feeding on diverse groups of both phyto- and zooplankton (Lukić et al., 2018).

2.3 | Feeding experiments under laboratory conditions

2.3.1 | Cultivation of *B. orientalis* for feeding experiments: laboratory population

To hatch animals, sediment containing resting eggs was collected from a soda pan, Oberer Stinkersee (47°48′49.4″N 16°47′34.4″E), and stored dry at 4°C in the dark for several months. After sieving and centrifuging the sediment according to the sugar flotation method (Marcus, 1990; Onbe, 1978), we incubated the eggs for hatching in a climate chamber, with a light regime 16L:8D and a temperature of 18°C. Resting eggs were incubated in a medium prepared from sodium hydrogen carbonate and distilled water (i.e. artificial soda water, 0.5 g $NaHCO_3$ per L water; conductivity 0.5 mS/cm). Once the animals started to hatch, we picked them out manually and transferred them to larger plastic containers (21 L) filled with artificial soda water and with constant aeration. A small amount of dry sediment from their natural habitat was added to the medium, to promote bacterial growth (that can serve as food for anostracan nauplii; final conductivity of medium around 1 mS/cm). We fed anostracans daily with a mix of algal food (*Cryptomonas* sp., *Scenedesmus* sp., *Chlamydomonas* sp.), which was at a later stage combined with zooplankton (the rotifer *Brachionus asplanchnoidis*, the cladoceran *M. brachiata*, and the copepod *A. spinosus*), constantly maintaining a sufficient amount of food for animals in the culture. Animals were considered adults once mating was observed (around 4 weeks old in the case of the laboratory population).

2.3.2 | Collection of *B. orientalis* for feeding experiments: field population

The anostracans raised in the laboratory (mean ± *SD* of the body length 1.44 ± 0.13 cm) were smaller compared to those collected in the field (2.46 ± 0.22 cm); therefore, in a second set of experiments, we collected full-sized adults in the field to verify data obtained with laboratory animals. For these experiments, live animals were collected from Mittlerer Stinkersee (47°48′27.5″N 16°47′19.5″E) during spring 2017. After collection from the field, the population was kept and maintained the same way as the population hatched in the climate chamber.

2.3.3 | Experimental design and food types

The zooplankton groups used in the experiments as food were also collected live on the field in the Seewinkel area (47°48′49.4″N 16°47′34.4″E) and cultivated in the laboratory during the experiments. In the predatory feeding tests, two typical members of soda pan zooplankton communities were used (Horváth et al., 2014; Tóth et al., 2014): a copepod (*A. spinosus*, 20 individuals in 70 ml) and a rotifer (*B. asplanchnoidis*, 100 individuals in 70 ml). The zooplankton prey concentrations were comparable to the

zooplankton densities in their natural habitats in previous seasons (data not shown).

We offered two different sized algae as food in the herbivory feeding tests. A coccoid green algae *Mychonastes* sp. (Sphaeropleales; diameter 2–3 μm) was used as picoplankton (the dominant size group of phytoplankton in soda pans; Felföldi, Somogyi, Márialigeti, & Vörös, 2009; Vörös, Balogh, & Boros, 2005), and the green flagellate *Chlamydomonas* sp. (Chlamydomonadales), which represented a larger unicellular food (7–18 μm length). The algal food concentration was at least 4 × higher than the concentration considered as saturating food abundance for *Daphnia magna* (Porter, Gerritsen, & Orcutt, 1982), that is 2 mg/L dry weight in the feeding experiments with the laboratory animals and 7 mg/L with the anostracan population from the field.

We performed short-term feeding experiments at multiple turbidity levels (from 40 min to 4 hr depending on the prey type and anostracan population such as in Lukić et al., 2018). We applied a logarithmic scale covering the entire range of turbidity levels in soda pans during spring (Horváth, Vad, Voeroes, et al., 2013a), when *B. orientalis* occurs (1–10,000 mg/L TSS concentrations; for duration, food concentration, number of replicates and turbidity levels see Table S1). The number of replicates was generally higher in the carnivory feeding experiments compared to the herbivory feeding experiments, because of the previously noticed higher variation between replicates (Lukić et al., 2018).

To create *turbidity*, we sieved the fine sediment (<250 μm) from a soda pan, Oberer Stinkersee (this is the same pan that was the source of the anostracan eggs used for the laboratory-raised population). The chosen soda pan is turbid and the characteristic greyish-white colour is caused by the high amount of suspended mineral particles in the water column (Boros et al., 2013). The sediment was dried and sterilised in an oven at 90°C (to avoid the growth of bacteria or algae). We added the selected amount of sediment (1–10,000 mg/L TSS; Table S1) to distilled water. Adding different amounts of dry sediment can result in slightly different salinity and pH levels in the treatments. To keep them the same at all turbidity levels, we added sodium hydrogen carbonate ($NaHCO_3$, one of the most dominant compounds in the natural habitats of *B. orientalis*; Boros, Horváth, Wolfram, & Vörös, 2014; Horváth, Vad, Vörös, & Boros, 2013a) to the lower turbidity treatments until salinity was equal to the treatment with the highest concentration of TSS (10,000 mg/L; final conductivity 1.6 mS and pH 8.4). As experimental units, transparent plastic vials of 100 ml total volume were used, filled up with 70 ml of the medium. In all experiments, two adult *B. orientalis* females were used per replicate. All experiments were run in a climate chamber during daytime under the same conditions used to maintain the algal and animal cultures (18°C). For all treatments and food items, controls (without *B. orientalis*) were run in parallel. To avoid algal sedimentation, medium was gently mixed in the algal feeding experiments (both controls and vials with *B. orientalis*) at regular intervals (30 min) and immediately before sampling phytoplankton for quantification.

In the first set of experiments, we tested how turbidity affects the ingestion rates of anostracans for all four prey types separately (*Mychonastes*, *Chlamydomonas*, *Brachionus*, and *Arctodiaptomus*) along an experimental turbidity gradient represented by five levels (1, 10, 100, 1,000, and 10,000 mg/L TSS). We then performed a second set of experiments employing *B. orientalis* collected as adults on the field, in order to test whether the effect of turbidity depends on adult size (animals from the field were considerably larger, see above). Here, we repeated the feeding experiments with three prey types individually (*Mychonastes*, *Chlamydomonas*, and *Arctodiaptomus*) and then tested for selective feeding using two food items (*Chlamydomonas* and *Arctodiaptomus*) provided in a mixture. In the second set of experiments, we used three turbidity levels (1, 100, and 10,000 mg/L TSS) except for *Arctodiaptomus* (five levels; see Table S1).

2.3.4 | Calculation of biomass and ingestion rates

We calculated the dry weight biomass per cell from biovolume based on (Bowie et al., 1985; Vadstein, Jensen, Olsen, & Reinertsen, 1988). Biovolume of the algal food was approximated by measuring cellular dimensions and approximating them to simple geometrical bodies (sphere for *Mychonastes* sp. and depressed ellipsoid for *Chlamydomonas* sp). In zooplankton, *B. asplanchnoidis* and *A. spinosus* biomass per individual were calculated from the average weight of dried individuals (0.5 μg per individual for *B. asplanchnoidis* and 13.5 μg per individual for *A. spinosus*).

Biomass ingestion rate per anostracan in the experiments was calculated based on the equations from Frost (1972) and Marin, Huntley, and Frost (1986), assuming that food concentrations were below saturating concentration:

$$M = \frac{gC_0Vm}{N},$$

where M is ingested biomass per animal and time (in μg/h); g, grazing coefficient; C_0, phytoplankton cell concentration or concentration of zooplankton offered as food at the beginning of experiment (in cells/ml); V, volume of medium (in ml); m, average biomass (in μg) per phytoplankton cell or zooplankton individual; and N, number of anostracans per vial. The grazing coefficient (g) was calculated for all food types according to the formula:

$$g = k - \frac{\ln(C_t) - \ln(C_0)}{t},$$

where C_0 is initial cell concentration of phytoplankton or initial concentration of zooplankton offered as food at the beginning of the experiment; C_t, final cell concentration of phytoplankton or final concentration of zooplankton offered as food at the end of the experiment, k, growth rate based on the change of algal concentration in controls (applicable for phytoplankton); and t, duration of the experiment (in hr) (Marin et al., 1986).

2.4 | Trophic position in the natural environment: field sampling and sample analyses

2.4.1 | Field sampling and laboratory measurements

In April 2018, zooplankton and fully adult anostracans were collected in nine soda pans to determine the stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values of *A. spinosus* and *B. orientalis* in relation to turbidity. The anostracans were collected with a push net (mesh size of 2 mm), while water was collected with a plastic beaker and sieved through a plankton net (mesh size of 100 μm) for zooplankton. Samples of *B. orientalis* and zooplankton were rinsed with distilled water (to remove the sediment and other particles suspended in the water column) and immediately frozen on dry ice and, after being transported to the laboratory, stored at −80°C. We also collected additional zooplankton samples for species identification and for enumerating zooplankton density. For this, 20 L of water was sieved through the 100-μm plankton mesh and the sample was fixed in 70% ethanol. Animals were identified and quantified under stereo and light microscope in the laboratory.

Environmental parameters (water depth, conductivity, pH, TSS, chlorophyll *a* concentration, total nitrogen [TN], and TP) and zooplankton density were analysed 2 weeks prior to the collection of animals and again on the day of anostracan collection (except for zooplankton density). To measure the amount of TSS in soda pans, water samples were collected and for each pond 1–50 ml water (depending on turbidity) was filtered through a pre-weighted GF/F filter immediately after returning from the field. Filters were dried in the oven at 60°C for overnight and measured again. The TSS concentration was the difference between the dry weight of the filters before and after filtering, divided by the volume of water filtered through the filters.

2.4.2 | Stable isotope analysis

We used *B. orientalis* individuals (both males and females) of 2.0–2.7 cm body length, which was the largest anostracan size group found in soda pans during the sampling. We decided to use one of the zooplankton prey groups as a baseline (Jardine, Kidd, & Fisk, 2006), because in a previous sampling campaign we found the $\delta^{15}N$ and $\delta^{13}C$ values of seston unreliable (due to the high variation among the replicates; data not shown). *Arctodiaptomus spinosus*, the IG prey of anostracans, was one of the dominant zooplankton taxa, being present in all of the nine soda pans. Therefore, we isolated *Arctodiaptomus* under a stereo microscope from the thawed zooplankton samples in the laboratory and used them as a baseline for the relative trophic position of anostracans. Calanoid copepods are mostly feeding on algae, protozoans and rotifers (Kleppel, 1993; Lapesa, Snell, Fields, & Serra, 2004). Since *Arctodiaptomus* is an omnivore, the relative trophic position of *Branchinecta* should range from −0.5 (being purely herbivorous) to 0.5 (being a pure primary predator). Isolated *Arctodiaptomus* and *Branchinecta* specimens were rinsed once again with distilled water, then freeze-dried and 0.3 mg of a homogenised sample was placed in tin caps (three replicates for each animal group and soda pan) as part of standard sample preparation procedure to analyse nitrogen stable isotope composition by using the Elemental Analysis Isotope Ratio Mass Spectrometry (EA-IRMS; EA—Thermo Scientific™ FLASH 2000 HT™; IRMS—Thermo Scientific™ Delta V™ Advantage). For both *Arctodiaptomus* and *Branchinecta*, the whole body of the animals was used in the analyses, which is a regularly used method for both zooplankton (reviewed in Feuchtmayr & Grey, 2003) and anostracans (Sánchez et al., 2013). Relative trophic position of *Branchinecta* was determined based on the following equation (modified from Hobson & Welch, 1992; Jardine et al., 2006):

$$RTP_{B.\,orientalis} = \frac{\delta^{15}N_{B.\,orientalis} - \delta^{15}N_{A.\,spinosus}}{\Delta^{15}N},$$

where $\delta^{15}N$ is the stable isotope ratio of nitrogen and $\Delta^{15}N$ is the *enrichment factor* representing the increase in $\delta^{15}N$ from one trophic position to the next, for which we used the general value of 3.4‰ (Fry, 2006; Jardine et al., 2006).

2.5 | Statistical analyses

Negative biomass ingestion rates were set to zero prior to statistical analysis of grazing rates (Boersma et al., 2016; Nejstgaard, Naustvoll, & Sazhin, 2001). Moreover, in a few cases with *Brachionus* as food, all offered rotifers were ingested, setting the final food concentration at the end of the experiments to zero. Since the final concentrations are log-transformed in our equation to calculate the grazing coefficients, this would not have resulted in a meaningful value (Legendre & Legendre, 1998). Therefore, in these cases we decided to use a small non-zero value of 0.25 rotifer per experimental vial (mean between 0 and 0.5, a range that should be rounded to 0). TSS values were also log-transformed for the analyses. We fitted linear regressions (LR) to analyse feeding efficiency (expressed in biomass ingestion rates) as a function of turbidity (log-transformed TSS). We used a standardised regression coefficient (*lm.beta* package; Behrendt, 2014) to compare the effect of turbidity on different food types. As variation in the experimental data tended to scale with turbidity, we tested for heteroscedasticity (Breusch–Pagan test, *lmtest* package; Zeileis & Hothorn, 2002). In cases where this test was significant (*Mychonastes* prey with laboratory-raised anostracans, *Chlamydomonas* prey with field anostracans, and *Chlamydomonas* and *Chlamydomonas* + *Arctodiaptomus* prey in the mixed feeding of field anostracans, Table 1), we performed the Box–Cox (BC) transformation implemented with the *caret* package (Kuhn, 2008) on the biomass ingestion rate data set and then repeated the LR test. In every case, heteroscedasticity was non-significant after transformation.

To compare the differences between the slopes of two selected prey types (*Chlamydomonas* and *Arctodiaptomus* in all the three experiments) we fitted LR including two treatments and their interaction (turbidity*prey) in each of the three sets of experiments. If the

TABLE 1 Linear regressions fitted for the feeding experiments: individual prey offered to the laboratory-raised population of *Branchinecta*, individual prey offered to the population of *Branchinecta* from the field, and mixed prey (*Chlamydomonas* + *Arctodiaptomus*) offered to the population of *Branchinecta* from the field

		No transformation			Box-Cox transformation		
	Food	β	R^2	*p*	β	R^2	*p*
Laboratory population of *Branchinecta*; individual prey	*Mychonastes*	−0.63	0.35	.012	−0.72	0.48	.002
	Chlamydomonas	−0.84	0.69	<.001	–	–	–
	Brachionus	−0.47	0.19	.017	–	–	–
	*Arctodiaptomus**	−0.18	−0.01	.386	−0.17	−0.01	.403
Population of *Branchinecta* from the field; individual prey	*Mychonastes*	−0.72	0.45	.028	–	–	–
	Chlamydomonas	−0.51	0.23	.004	−0.52	0.25	.003
	Arctodiaptomus	−0.14	−0.00	.327	–	–	–
Population of *Branchinecta* from the field; mixed prey	*Chlamydomonas*	−0.53	0.25	.003	−0.44	0.16	.015
	*Arctodiaptomus**	−0.37	0.10	.046	−0.29	0.05	.123
	Chlamydomonas + *Arctodiaptomus*	−0.72	0.50	<.001	−0.75	0.54	<.001

β is the standardised regression coefficient. Missing values ('–') indicate that no Box–Cox transformation was performed for the data due to non-significant outcomes of the Breusch–Pagan test which indicated a lack of heteroscedasticity. Asterisks indicate experiments where the Breusch–Pagan test was marginally significant (.05 < *p* < .1).

Breusch–Pagan test was significant in this step, a robust LR (lm_robust() function in the *estimatr* package; Blair, Cooper, Coppock, Humphreys, & Sonnet, 2019) was chosen over a regular LR (this was necessary in the experiments with laboratory-raised anostracans and the mixed food experiments with field anostracans).

For stable isotope analyses, we first checked the effect of turbidity on the $\delta^{15}N$ values of *Arctodiaptomus* and *Branchinecta* in two separate LR models. Then to study the relationship between the relative trophic position of anostracans and environmental parameters, we selected the best linear regression model explaining relative trophic position. For that, we used a stepwise regression with forward selection implemented with the *caret*, *leaps* (Lumley & Miller, 2017) and *MASS* (Venables & Ripley, 2002) packages. As predictors in the null model of the stepwise regression, we included TSS, conductivity, water depth, zooplankton density, and TN, including both measurements 2 weeks prior and on the day of the anostracan sampling (except zooplankton density). All predictors except conductivity and TN were log-transformed. Total phosphorus concentration and chlorophyll *a* were not included in the initial model because they both showed strong significant positive correlation with TSS at both time points, which is a general pattern in these habitats (see also Horváth et al., 2014). Model selection was based on mean absolute error and root mean squared error criteria. We tested the effect of the resulting best predictor (TSS) on the relative trophic position with an LR.

We used $\delta^{15}N$ and $\delta^{13}C$ values to calculate the area of the convex hull (i.e. trophic niche, as in Layman, Quattrochi, Peyer, & Allgeier, 2007) of the soda pan communities (*Arctodiaptomus* + *Branchinecta*, altogether 6 samples per soda pan) using the *SIBER* package (Jackson, Inger, Parnell, & Bearhop, 2016). We log-transformed the obtained trophic niche values and then tested their relationship with turbidity (log-transformed TSS measured 2 weeks prior anostracan sampling) with an LR model. All data were analysed in R (R Core Team, 2014).

3 | RESULTS

3.1 | Feeding experiments

In the algal feeding experiments (for the ingestion rates see Table S2), turbidity had a similar significant negative effect on the ingestion rates of both anostracan populations, the laboratory-raised anostracans (Table 1 and Figure 1a,b) and the ones from the field (Table 1 and Figure 2a). *Mychonastes* was ingested at rates similar to those found in the case of the laboratory population (consisting of somewhat smaller animals), while ingestion rates on *Chlamydomonas* appeared to be higher in the anostracans from the field. Ingestion rates on *Chlamydomonas* were overall higher (with close to one order of magnitude in a few treatments) than on *Mychonastes* for both the population from the field and the laboratory-raised anostracans.

The effect of turbidity on the carnivory of *Branchinecta* was not detectable in most cases. We did not find a significant effect of turbidity on feeding on *Arctodiaptomus* either in the laboratory-raised (Figure 1d and Table 1) or in the field population (Figure 2b and Table 1). Turbidity only had a significant negative impact on the ingestion of *Brachionus* (Figure 1c and Table 1).

In the feeding experiments with mixed food (algae + zooplankton offered simultaneously to the field population), results were similar to the individual experiments with both anostracan populations (Table S2). Turbidity had a significant negative effect both on herbivorous and carnivorous feeding without BC transformation (Figure 3a), but after BC transformation, only the effect on herbivorous feeding stayed significant (Table 1). Overall, total biomass

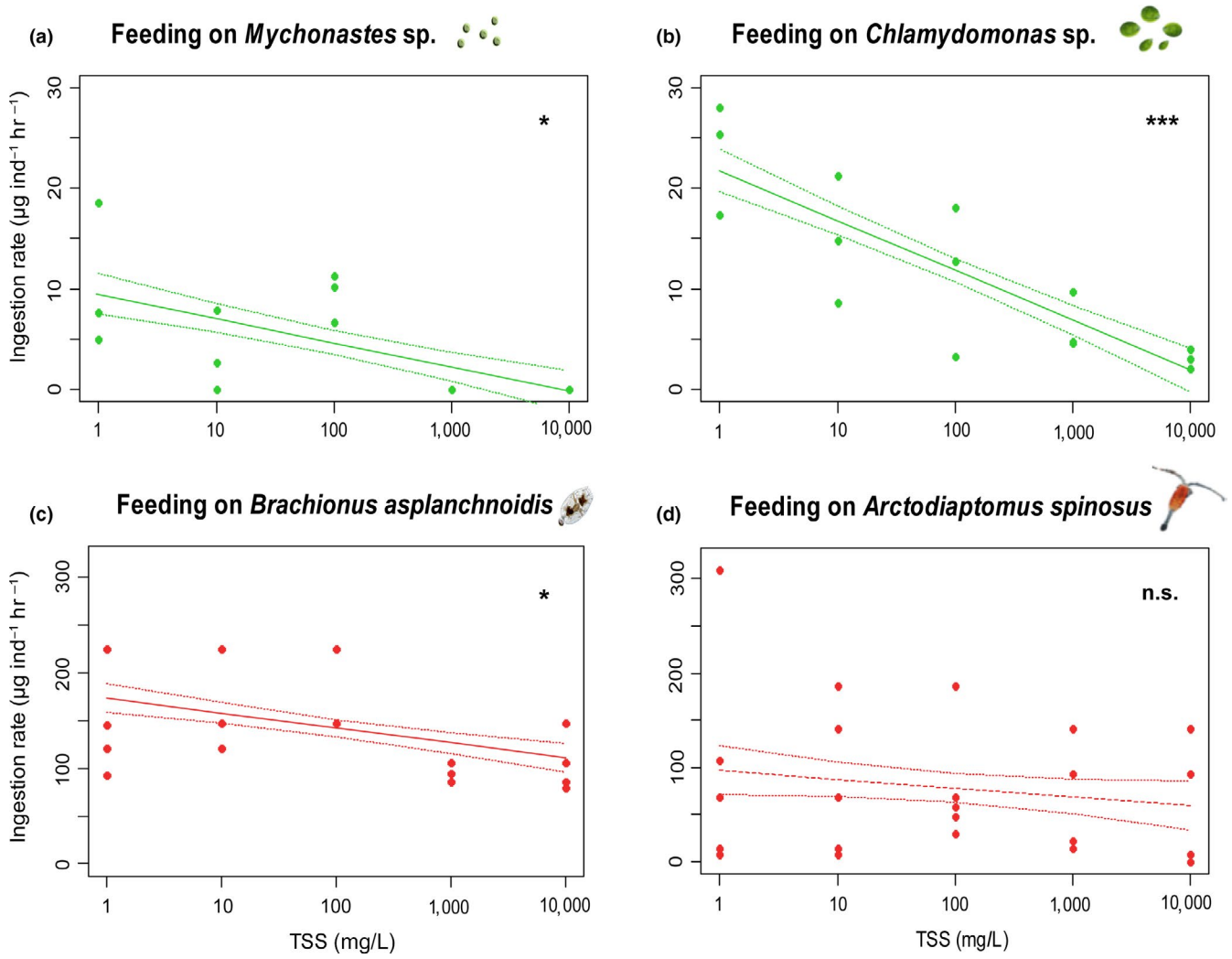

FIGURE 1 Biomass ingestion rates of *Branchinecta orientalis* (laboratory-raised specimens) on the four different food groups. Effect of turbidity was significantly negative for herbivorous feeding on (a) *Mychonastes* sp. (linear regressions, LR: R^2 = 0.35, p = .012), (b) *Chlamydomonas* sp. (LR: R^2 = 0.69, p < .001), and carnivorous feeding on rotifer (c) *Brachionus asplanchnoidis* (LR: R^2 = 0.19, p = .017) but not significant for carnivorous feeding on calanoid copepod (d) *Arctodiaptomus spinosus* (LR: R^2 = −0.01, p = .386) [Colour figure can be viewed at wileyonlinelibrary.com]

ingestion rates (sum of all algae + zooplankton biomass consumed per experimental vial) were also decreasing with increasing turbidity (Figure 3b; Table 1). At the same time, the ratio of ingested food types (based on biomass) reversed with increasing turbidity, with a higher ratio of algal food ingested in clear compared to a higher ratio of animal food in turbid water (Figure S1).

By directly comparing the regression slopes for three experimental groups (feeding experiments with the laboratory-raised anostracans, individual and mixed feeding experiments with anostracans from the field) across food type treatments, we found significant differences between the slopes of *Chlamydomonas* and *Arctodiaptomus* prey in the individual feeding experiments of anostracans from the field (the turbidity*prey interaction in LR: t_{76} = −2.11, p = .038). This interaction was not significant in the laboratory-raised population (t_{36} = 0.35, p = .724) or the mixed feeding experiment with the anostracans from the field (t_{56} = −1.68, p = .097).

3.2 | Trophic position of anostracans in their natural habitats

There was a significant correlation between the δ^{15}N values of anostracans and turbidity, while this was not the case for copepods (Figure 4a). The relative trophic position of *Branchinecta* relative to *Arctodiaptomus* (omnivore) ranged from −0.39 (equivalent to the position of primary consumers, implying the dominance of herbivorous feeding on phytoplankton) to 0.68 (position of secondary consumers, implying the dominance of carnivorous feeding on primary consumers). The relative trophic position of anostracans was best explained by the mean turbidity of their habitats measured 2 weeks before sampling for the stable isotope analysis (Table S3), although the relationship in the following LR was not significant (Figure 4b, p = .152).

The log-transformed trophic niche values of soda pan communities (*Arctodiaptomus* + *Branchinecta*) showed a significant positive

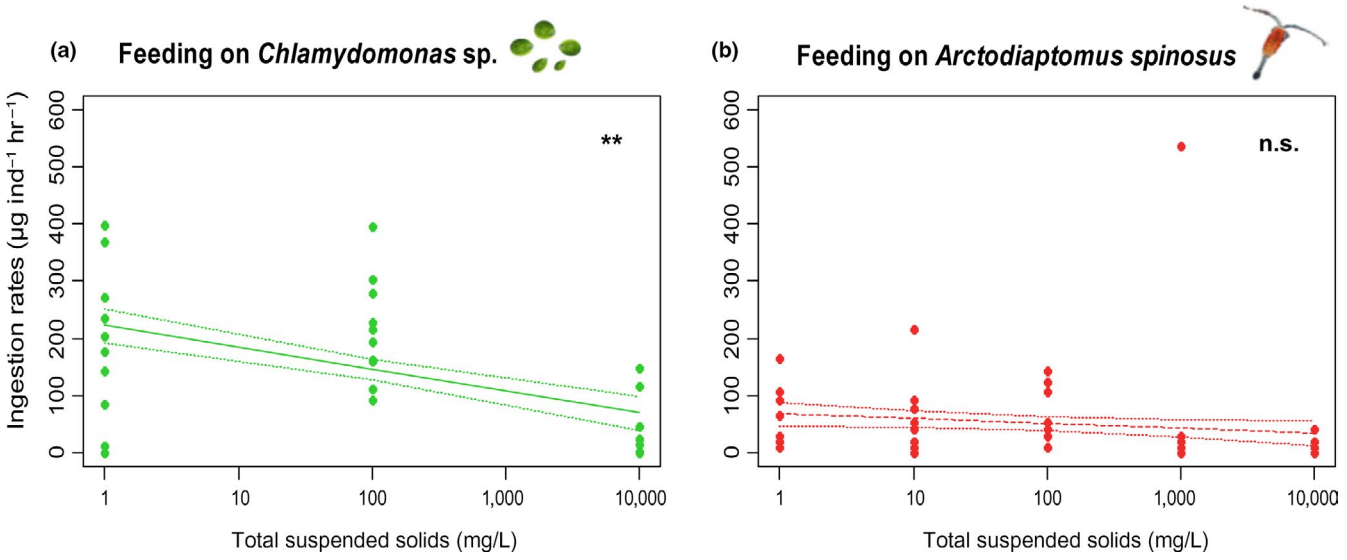

FIGURE 2 Biomass ingestion rates of *Branchinecta orientalis* (specimens collected from the field) in the single-food experiments. In case of (a) herbivorous feeding on the algae *Chlamydomonas* sp. biomass ingestion rates decreased significantly along the turbidity gradient (linear regressions, LR: R^2 = 0.23, p = .004), while in (b) carnivorous feeding on the zooplankter *Arctodiaptomus spinosus*, no significant pattern was detected (LR: R^2 = −0.0004, p = .327) [Colour figure can be viewed at wileyonlinelibrary.com]

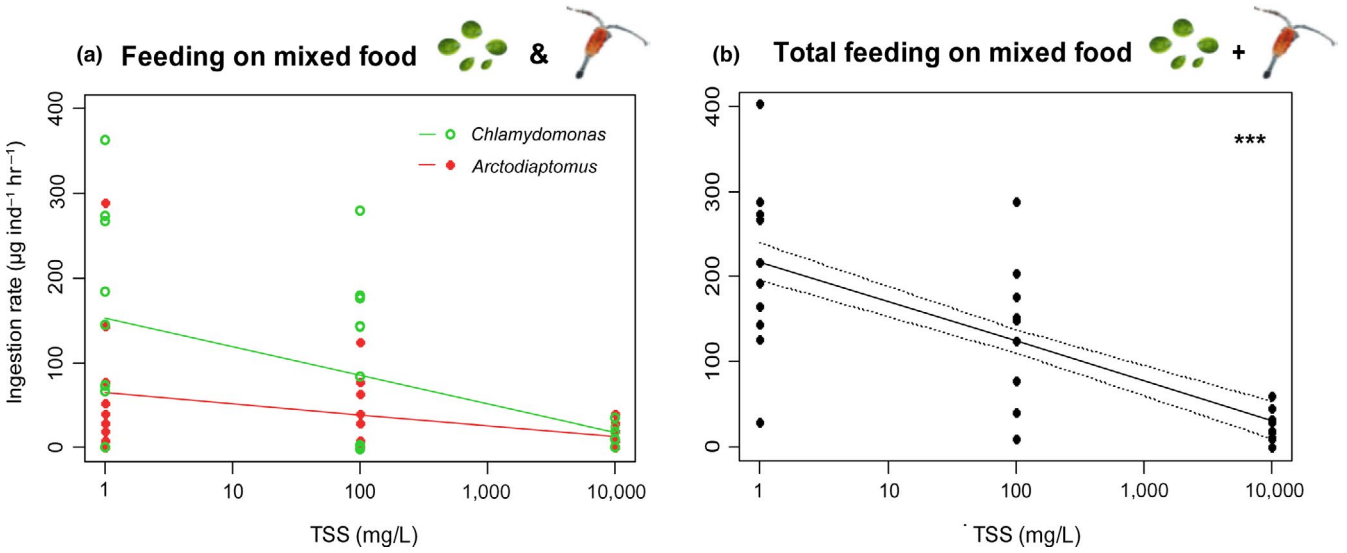

FIGURE 3 Biomass ingestion rates of *Branchinecta orientalis* (specimens collected from the field) in the mixed food experiment along the turbidity gradient. (a) Ingestion rates for *Chlamydomonas* sp. (linear regressions, LR: R^2 = 0.25, p = .003; green empty circles and green regression line) and *Arctodiaptomus spinosus* (LR: R^2 = 0.10, p = .046; red filled circles and red regression line). (b) Total ingestion rate in the same experiment (algae + zooplankton; LR: R^2 = 0.50, p < .001) [Colour figure can be viewed at wileyonlinelibrary.com]

correlation with the same measurement of turbidity (Figure 4c), indicating that the trophic role of anostracans became more distinct from the copepods as turbidity increased, which widened the isotopic niche of the community.

4 | DISCUSSION

Turbidity reduced the feeding rates of *Branchinecta* on both algal prey types (*Mychonastes* and *Chlamydomonas*) in all experimental setups. Although the ingestion rates on *Chlamydomonas* in the clear water treatment were much higher in the large anostracan population (compared to the smaller population raised in the laboratory; see Figures 1b and 2a), the overall response to the turbidity treatment was the same. In contrast, turbidity had no significant to weak effect on the ingestion of zooplankton. This altogether implied a shift in the IGP system, with an increasing relative importance of carnivory towards high turbidity. The observed increase in anostracan δ^{15}N values and relative trophic position, as well as the community trophic niche, match the experimental results. Thus, our results

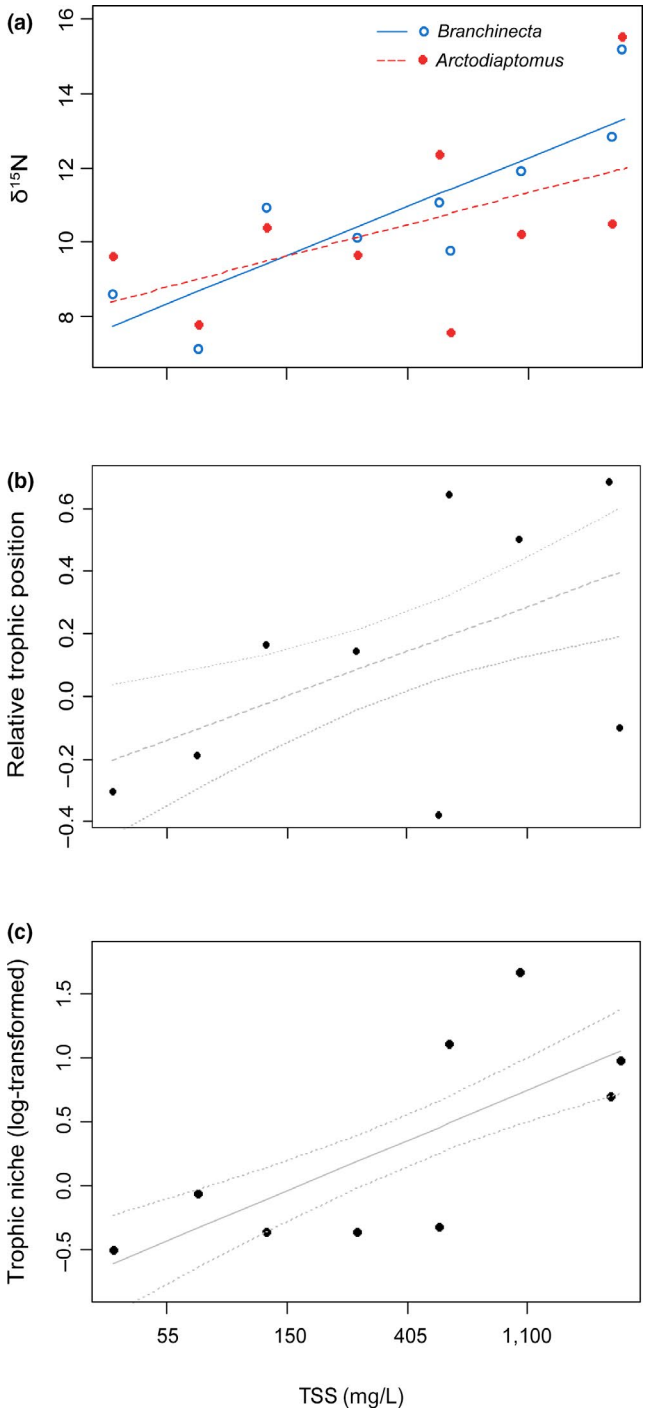

FIGURE 4 Stable isotope data of *Arctodiaptomus spinosus* and *Branchinecta orientalis* from nine soda pans. (a) $\delta^{15}N$ values of *A. spinosus* (linear regressions, LR: $R^2 = 0.19$, $p = .133$; red filed circles and red regression line) and *B. orientalis* (LR: $R^2 = 0.69$, $p = .003$; blue empty circles and blue regression line) along the turbidity gradient (represented by log-transformed total suspended solids [TSS]). TSS in the soda pans measured 2 weeks prior to animal sampling for stable isotope analysis. (b) Relative trophic position of *B. orientalis* (compared to *A. spinosus*) along the turbidity gradient (log-transformed TSS; LR: $R^2 = 0.16$, $p = .152$). Trophic position is calculated in relation to *A. spinosus* (intraguild [IG] prey), where 0 indicates when they occupy the same position (competition between IG predator and IG prey) whereas 1 indicates that the position of *B. orientalis* is one level higher (implying the predominance of a predator–prey relationship between IG predator and IG prey). (c) Convex hull area (i.e. trophic niche) of the soda pan communities (*B. orientalis* + *A. spinosus*) along the turbidity gradient (both variables were log-transformed; LR: $R^2 = 0.46$, $p = .026$) [Colour figure can be viewed at wileyonlinelibrary.com]

showed that inorganic turbidity modulated the strength of trophic relationships between an IG predator and its prey, which implies an important community shaping role of turbidity in aquatic systems.

4.1 | Effect of turbidity on anostracan feeding

Up to now, very little is known on the possible environmental effects on the ingestion rates in anostracans. Herbivorous feeding (i.e. filter-feeding on algae) have been shown to be affected by salinity (Sánchez, Paredes, Lebouvier, & Green, 2016) and water quality (Brendonck, 1993), but the effect of inorganic turbidity was so far unknown. For non-selective filter feeders such as cladocerans, high amounts of TSS usually lead to the ingestion of increased amounts of inorganic particles and consequently a reduction in ingested algae (Arruda, Marzolf, & Faulk, 1983; Hart, 1988). Another possible effect is the mechanical inhibition of food collection by inorganic particles, which has also been documented for filter feeders (Kirk, 1991b). Our observations on live anostracans collected from the field and used in our feeding experiments rather suggested the first effect (ingestion of high amounts of inorganic particles), as the intestines of animals feeding in turbid environments were greyer (D. Lukić, personal observation). In addition to a lower ingestion of algae, we also recorded a decrease in the ingestion rate on the rotifer *Brachionus*. *Brachionus* is a relatively large rotifer species (180–500 μm body length), but a very slow swimmer. Therefore, some authors already considered feeding on rotifers as one way of filter-feeding (as in feeding on algae) rather than true predatorial behaviour (Dumont, Ali, Sarma, & Mertens, 1994), which is also supported by our results.

Many anostracan species live in turbid waters (Daborn, 1977; Hancock & Timms, 2002; Horváth, Vad, Vörös, et al., 2013a). Based on the existing evidence, anostracans are presumably not visual predators (Boudrias & Pires, 2002; Rogers & Timms, 2017) and rely on other senses instead to locate their prey. Their antennae and other extremities are densely covered by setae (Boudrias & Pires, 2002; Rogers, Quinney, Weaver, & Olesen, 2006; Rogers & Timms, 2017), which are suggested to play an important role in tactile (as suggested for *Branchinella occidentalis*; Rogers & Timms, 2017) or chemosensory detection of prey (suggested for *Branchinecta* species; Boudrias & Pires, 2002). These are in agreement with our findings and could explain the weak to no effect of increased turbidity on carnivorous feeding on the largest and most motile prey (*Arctodiaptomus*) offered in our experiments. This implies that feeding on *Arctodiaptomus* probably happens via another mechanism of feeding (different from the filtration of algae and rotifers), which suggests that anostracans are able to use different feeding mechanisms—filter and predatory feeding—depending on the prey type.

In this study, the whole body of anostracans was used for stable isotope analysis, which integrates the information on food assimilated during the majority of the adult life of the studied organisms (Zanden, Clayton, Moody, Solomon, & Weidel, 2015). For anostracans, it would probably be around 4 weeks prior to our sampling (judged based on the size of anostracans and the time of ice break). However, local values of TSS can show extreme temporal changes in soda pans (see Table S4). For that reason, we included data on TSS (and the other available environmental parameters) from 2 weeks before the stable isotope sampling, and the 2-week prior TSS values were indeed the best predictors of the trophic position of *Branchinecta*. The results of the field test were in accordance with our laboratory experiments—the relative trophic position of *Branchinecta* rose with TSS, with an increase of one entire level from the most transparent to the most turbid habitat—implying that increased turbidity induced a shift in their feeding (indicating zooplankton as major prey in these cases). This suggests that turbidity acts as an important determinant of the strength of trophic relationships between anostracans and their prey (Figure 5). Moreover, the increasing amount of available food, algae, and zooplankton, along the turbidity gradient (which is a general pattern in our study systems, Horváth et al., 2014) might compensate for the overall decrease in total ingested biomass with increasing turbidity we observed in our experimental setup, where food levels were kept constant. This can eventually explain the high abundances of anostracans even in very turbid habitats (Boudrias & Pires, 2002; Boven, Vanschoenwinkel et al., 2008; Horváth, Vad, Vörös, et al., 2013a).

4.2 | Effect of anostracans on the community as an IG predator

Our results have further implications regarding the importance of anostracans as IG predators for the entire community. Anostracans can reach high densities in their habitats (Daborn, 1977; Horváth, Vad, Vörös, et al., 2013b; Vanschoenwinkel, Brendonck, Pinceel, Dupriez, & Waterkeyn, 2013; Vanschoenwinkel, Seaman, & Brendonck, 2010) and they act both as competitors and predators of smaller zooplankton (Jocque, Vanschoenwinkel, & Brendonck, 2010; Lukić et al., 2018; Waterkeyn et al., 2011), which suggests a high impact on the zooplankton community. Even though *B. orientalis* hatches very early after inundation/ice break (Lukić, Vad, & Horváth, 2016; Petkovski, 1991), it is probably predominantly herbivorous in the early stages of its life (similar to other anostracans; Daborn, 1975; Fryer, 1983), which gives some time for zooplankton communities to establish at the beginning of the wet phase of their habitats. Moreover, anostracans disappear before temporary ponds dry out, while many zooplankton species occur throughout the whole wet season (Horváth, Vad, Vörös, et al., 2013a; Jocqué, Riddoch, & Brendonck, 2007; Tóth et al., 2014; Vanschoenwinkel, Waterkeyn, et al., 2010), which overall provides a temporal refuge for zooplankton (Kratina et al., 2012). In addition, anostracans do not feed on the largest zooplankton such as adult *D. magna* (they are only susceptible to anostracan predation in the earliest stages of their life, Lukić et al., 2018). In this way, anostracans could even promote the maintenance of larger *Daphnia* in the communities through decreasing the densities of their competitors, that is smaller zooplankton taxa.

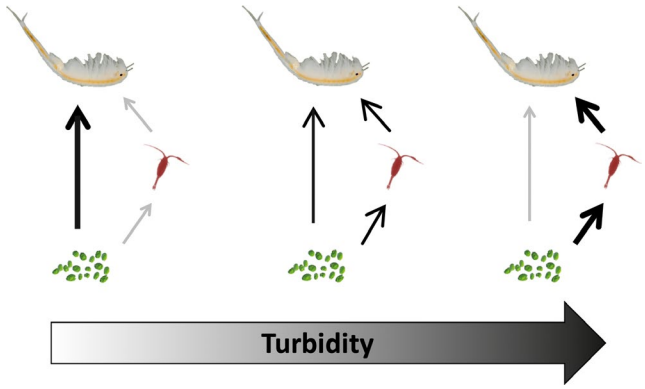

FIGURE 5 A schematic representation of the changes in the relative strength of interactions in the studied intraguild predation system along the turbidity gradient, with anostracans as intraguild predators, zooplankton as intraguild prey, and phytoplankton as shared prey [Colour figure can be viewed at wileyonlinelibrary.com]

4.3 | Influence of turbidity on the IGP system

Changes in inorganic turbidity can lead to significant shifts in community composition (Teffera et al., 2018; Zhou et al., 2018). According to our results, suspended inorganic particles create a refuge for smaller prey of anostracans (algae and small zooplankton), comparable to structured habitats providing a refuge for IG prey (although the direct mechanism is different) (Janssen et al., 2007). Similar phenomena were shown in case of visual predators (planktivorous fish) and their prey (zooplankton), where increased levels of turbidity or the deeper dark strata of lakes provided a refuge for zooplankton (the latter via diurnal vertical migration of zooplankton) (Gardner, 1981; Vinyard & O'Brien, 1976). Furthermore, turbidity might also affect trophic relationships beyond the boundaries of aquatic habitats as experimental evidence showed that increased amounts of detritus particles can inhibit the filtration rate of filter-feeding waterbirds such as shovelers (Gurd, 2007).

At the same time, the effect of turbidity on the IGP system of temporary ponds is more complex. Our results show that turbidity probably does not affect the predation efficiency of anostracans on the IG prey (zooplankton) considerably, but it rather decreases competition for the shared resource (phytoplankton). We found that grazing on phytoplankton was very close to 0 in the most turbid treatments in our experiments, and the relative trophic position of anostracans similarly implied a predominantly carnivorous feeding in turbid habitats. As chlorophyll *a* concentrations significantly increase along the turbidity gradient in soda pans (Horváth et al., 2014), we can exclude that the reason for the predominantly carnivorous feeding of anostracans was resulting from limited amounts

of phytoplankton available as food. In temporary pond systems with anostracans as IG predators, turbidity does not provide efficient refuge for zooplankton (due to probably non-visual predation of anostracans), but it decreases their grazing pressure on phytoplankton (Figure 5), which can indirectly benefit zooplankton due to the higher phytoplankton (food) abundance in turbid ponds (Horváth et al., 2014). In hypertrophic systems such as soda pans (TP 67–4,177 μg/L in spring 2018), the IG prey would otherwise be prone to extinction (Diehl & Feissel, 2001). Turbidity and productivity are typically correlated in soda pans (this study; Horváth et al., 2014), which suggests the importance of turbidity as a stabilising factor in this part of the food web.

5 | CONCLUSIONS

Our results show that inorganic turbidity can alter trophic relationships through the feeding of an IG predator (anostracans in this study). This also implies a possible community shaping role of turbidity on plankton communities, with the strength of top-down control on the different groups varying with turbidity. In addition to the effect on the feeding of anostracans, other taxonomic groups are also likely to be directly affected, depending on their feeding type. For example, the ability of copepods to cope with increased turbidity better than cladocerans (Dejen et al., 2004) could shape competitive interactions within the zooplankton communities and help to sustain copepod dominance in highly turbid soda pans (Horváth et al., 2014). The global presence of anostracans in turbid ponds could also at least partly stem from to their ability to feed on different prey types and to switch between multiple feeding mechanisms. Furthermore, amphibians and waterbirds feeding from temporary ponds could also be affected by changes in inorganic turbidity and subsequent changes in prey availability (Gurd, 2007). Therefore, the consequences of increased turbidity are expected to be complex, acting on multiple trophic levels.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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